GLOBEC

Global Ocean Ecosystems Dynamics

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Theory and Modeling in GLOBEC: A First Step

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Report to the GLOBEC Steering Committee
from the Working Group on Theory and Modeling

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I. GLOBEC. THE RESPONSE OF MARINE ECOSYSTEMS TO GLOBAL CHANGE

Evidence continues to accumulate that the environment of our planet is changing (Mitchell, 1989). The change is not localized, but extends from the tropics to the poles; it is apparent in the atmosphere, on land, and in the ocean. Some of the shifts are thought to be anthropogenic (ozone depletion in the Antarctic, increasing greenhouse gases, etc.); but paleoclimatic records also suggest that the earth has experienced at least some similar climatic changes in the past. We do not know whether these changes are cyclic or are long- term trends. We possess little information about the time scales of most of these shifts; some are relatively short -- several years (El Niño/Southern Oscillation events), while others may operate over very long time scales (incorporation of carbon into the deep sea: Broecker and Peng, 1982). The changes involve physical, geological, chemical, and biological processes. Scientists who study such processes are deeply engaged in the attempt to verify the existence and magnitude of these shifts. **But the greatest challenge will be to assess the direction and magnitude of the response of our planet's environment to these changes.**

What will be the impact of the changes in our global environment on the populations and communities of marine animals? GLOBEC (GLOBal ocean ECosystems dynamics) is an initiative proposed by the oceanographic and fisheries communities to answer this question. The GLOBEC approach is to develop fundamental information about the basic mechanisms that determine the abundance and distribution of marine animal populations and, most importantly, the variability of these populations about the average values. (We exclude populations of marine mammals as a primary focus because they are presently the subject of studies by several other international programs). Through understanding of these fundamental mechanisms reliable predictions of population changes in the face of a shifting global environment can be obtained. The most crucial aspect of the GLOBEC program is a close connection between studies of the physical environment and biological processes in the ocean. Indeed, the GLOBEC program is based on the assumption that the physical environment plays a crucial role in at least some of the life stages of most marine animals.

Why is this coupling of the biota to the physical environment so critical to our understanding of the impact of global change?

The answer to these questions turns on the fact that the great majority of marine animals have planktonic developmental stages which spend hours, and often several weeks, in the plankton. For example, many benthic invertebrates have larval stages that disperse widely (some more widely than others) away from the shore or bottom before they settle again as reproductive adults. Most nekton (large organisms that swim in the water column, like fish and squid) also have at least one planktonic stage during which they are largely at the mercy of the fluid motions in the sea. Finally, holoplankton, like the numerous copepods and other macrozooplankton, live entirely as planktonic forms. Accordingly, success of recruitment by larval and juvenile stages into reproducing adult stages does not depend on "biological" processes alone; that is, the transport of organisms into regions that are favorable or unfavorable to them plays a substantial, even dominant, role in the success of marine animal populations. Moreover, whether a region is favorable or unfavorable may depend not only on the availability of food or absence of predators, but also upon those physical features of the environment that transport the predators and food to, or away from, the organisms.

Furthermore, how the sea's physical and biological phenomena are coupled seems crucial to our initial attempts at understanding the impact of global change on marine animal populations. Scientists cannot predict with complete certainty what the impact of climatic changes will be on the various parameters that characterize the ocean and atmosphere. But many believe that, along with the hypothesized "greenhouse" warming, precipitation patterns will differ substantially from what we presently experience as "normal". Moreover, the high-latitude regions seem more sensitive than those at low latitude (Mitchell, 1989). These potential changes could have profound impacts on the marine phenomena that are important to planktonic forms in the sea, as several potential scenarios illustrate.

The coastal region of the Gulf of Alaska, for example, could be the site of such a large response. As precipitation patterns change, and global warming triggers rapid melting of permanent ice fields and retreat of glaciers, the amount of fresh water that enters the Gulf of Alaska is likely to be affected substantially. Studies are conclusive in their findings that the input of fresh water from the entire coastline of the Gulf is a critical component of the driving forces for the Alaska Coastal Current. Under a different precipitation regime the magnitude, even the direction, of this current could shift substantially. The effects of such a shift on the populations of various fish species could be large. For example, transport of eggs and larvae of the Alaskan Pollock could be affected. Walsh and McRoy (1986) modeled transport effects on this species in the adjacent Bering Sea, testing the hypothesis that years of reduced temperature (i.e., a climatic change) delay the development of copepod nauplii that are the primary food source for pollock larvae. They concluded that interannual population variability was consistent with the larval starvation hypothesis, and not advective effects. It would be interesting to compare this result to the Alaska Coastal Current case, where freshwater inputs and resultant currents can be substantially higher (Royer, 1982). Effects in regions where the coastal currents are driven by buoyancy derived from fresh water are not restricted to the Gulf of Alaska. Similar effects are seen in the coastal ocean off Norway. Mean currents in the Middle Atlantic Bight may be forced by freshwater inputs from the estuary of the St. Lawrence River. The Mississippi River has a measurable effect on the nearshore circulations of the entire Gulf of Mexico to the west of the Mississippi Delta, particularly in spring.

Another example involves oceanic fronts, where a sharp boundary exists between two neighboring water masses with different properties (e.g., differing temperatures, salinities, chlorophyll concentrations, speeds). Fronts are ubiquitous in the ocean, especially in the coastal ocean. There are at least five common types of fronts: shelf/slope (or shelf-break) fronts, upwelling fronts, tidal mixing (or shallow sea) fronts, estuarine fronts, and advective fronts (see Joyce [1983] for a thorough taxonomy). Biological activity is well known to be concentrated in frontal regions (Le Fevre, 1987). The positions of several of these frontal types (as well as local behavior at the front, like downwelling) may shift due to a changing global climatic regime, since most fronts can be strongly affected by winds. For example, the position of upwelling fronts will be under the control of coastal wind patterns, which are believed to be subject to climatic variation (Bakun, 1990). Indeed, paleoceanographic evidence indicates that coastal upwelling associated with the Asian Monsoon was more intense about 9000 B.P. during the maximum in Northern Hemisphere solar insolation (Mitchell, 1989). It seems reasonable to assume that associated upwelling fronts may have changed their positions in response to the different upwelling regime. In addition, the positions of estuarine fronts will be under the control of fresh water input to the estuarine system and, as a result, subject to variation with shifting precipitation regimes. The ecological role that the position of a particular front plays in the life history of a given organism is not, in general, known, but we know in that in certain cases this role can be very important (Tyler and Seliger, 1978).

Finally, that sea level is indeed rising at approximately 1-3 mm/yr seems to be supported by a growing consensus of scientists (Thomas, 1987). Extrapolated into the next 50 to 100 years this promises to have profound impacts on nearshore habitats. The width of the inner shelf environment (the inner shelf is the oceanic strip where the bottom significantly affects the flows -- formally, where the surface mixed layer approaches the bottom boundary layer) may greatly increase, especially in gently sloping bottom regions. It is likely that the mean surface gravity wave energy reaching the shore may decrease when distributed across a wider shelf; since transport in the wave zone -- both transverse to and along shore -- is controlled by surface waves, the transport of planktonic species (larvae, juveniles, etc.) may be substantially modified. The role that onshore transport plays in the recruitment of benthic invertebrate larval stages into reproductive adult populations is under intense scrutiny (Roughgarden et al., 1988). Most of our ecological understanding of these intertidal populations is based upon competitive interactions between adults and neglects transport (Connell, 1961; Paine, 1966). Whether this conventional view is correct for all populations is now being tested. And changing rates of transport due to rising sea level could have profound effects on the resolution of this question. Note that the time scales for competitive interactions to drive a single population to extinction in intertidal environments seem to be on the order of decades -- the same time scales for substantial rises in sea level.

The common thread in these three scenarios is that changing climate affects the physical phenomena in the sea, from the large scale, like changing inputs of fresh water modifying buoyancy-driven flows in the entire Gulf of Alaska, to the small scale, i.e., turbulence, mixing, and transport near shore and in fronts. Furthermore, because so many of the life stages of marine animals are planktonic, we expect to see the impacts of the changing "physics" on individual organisms, on the basic demographic parameters of marine populations, and on the communities of interacting populations in the sea. Repeating, then, the key to understanding how global change will affect marine populations lies in the planktonic nature of most stages of marine animals.

These conclusions dictate the two broad avenues a large program like GLOBEC must follow to address the impact of global change. First, comprehensive investigations of the effects of physical phenomena on marine populations must proceed at all three levels -- individual, population, and community -- because the effects of global change may be felt at all three. The basic mechanisms of population change (e.g., mortality through predation, or reproduction -- whose effects are summarized in life table parameters like l_x or m_x; Roughgarden [1979]) certainly occur at the individual level; nonetheless, there is no acceptable "statistical mechanics" of how individual level behavior can be used to uniquely determine population responses. And similarly, except in a few simple cases, the use of population level behavior to unambiguously determine community responses is not possible. Parenthetically, up to this point we have focused our discussion on the impacts of physical changes that will be felt by planktonic stages. But suitable recognition of the impact of interactions between non-planktonic individuals (e.g., micronekton, or benthic adults), or the impact of the physical environment upon such individuals, must be included in any comprehensive investigation. Second, after some consensus is reached about understanding of the basic mechanisms, scientists must address the question of predicting the future responses to climatic scenarios that researchers deem probable in the sea. Note that this last step assumes that compelling models have been constructed for the responses of individuals and populations within marine communities. It is to this modeling step that we now turn.

II. MODELING AND THEORY. A FIRST STEP.

The first step in any investigation is to determine what we know and what we don't about the topic. We propose that the first step in the GLOBEC program should be a modeling effort to determine how well we are able to put together our present knowledge of physical oceanography with the known population biology of marine organisms that have numerous, distinct, planktonic life stages. There have been few, if any, theoretical models that have successfully addressed this question (Wroblewski and Hofmann [1989] review population and community level efforts at meso- and ocean basin scales). We see this activity as a necessary first step to uncover the limits to our present ability to utilize existing information to predict the variability in marine populations.

This use of the modeling exercise to initiate GLOBEC is a "probe" -- an exploratory probe to determine where our knowledge breaks down. It should accompany any major investment in new technology and field studies, for solid progress in the coupled investigation of physical and biological processes. In this "probing" fashion we can uncover those crucial parameters about which we possess little empirical information; we can clarify the limits of our ability to perform a crucial measurement, suggesting where we need to develop new instrumentation. Furthermore, models can be very effective at suggesting additional variables that have greater power to discriminate among several previously "acceptable" explanations for an observed phenomenon. It becomes the first step in the iterative, interactive process between theory and experimental measurement.

There are also pragmatic reasons why theory and modeling studies should appear in the earliest stages in GLOBEC. Little "start up" time is required, as opposed to the efforts required for instrumentation development and design of multi-ship, multi-investigator field programs. Moreover, the cost of theoretical and modeling investigations is substantially less than that of other efforts.

We have identified three broad categories that are critical to explore: conceptual studies of simplification and predictability; prototype investigations of biological processes in idealized flow fields; and site-specific models. We elaborate upon these three categories below. We make no claim that these are the only categories that could be profitably explored: we are confident, however, that a synthesis of efforts in these three fields can yield especially useful results. Finally, we anticipate other future GLOBEC activities, especially experimental and field measurement programs. The initiative should include, at a minimum, a requirement for participation in a yearly workshop devoted to bringing together theoreticians and empiricists. Moreover, an additional modeling/theory gathering for those working at disparate tasks is a "must".

A. Conceptual Studies of Simplification and Predictability.

1. Simplification: scaling, pooling, and averaging.

Researchers have put little effort into the systematic dimensional analysis of equations that contain biological parameters (though see Wroblewski et al., 1975; Hofmann et al., 1980; Lyne, 1983). This lack is especially apparent for models that incorporate the higher trophic levels beyond phytoplankton. The technique has proven to be extremely powerful in physical oceanography (and in fluid dynamics, generally); one can predict with confidence that any coupled modeling effort will have to address the issue of the "proper" non-dimensionalization--the "proper" scaling--early on.

In many population models quantities are pooled; for instance, we refer to "phytoplankton" or "zooplankton", pooling all the phyto- or zooplankton species together. Age or size classes are averaged, or pooled, and equations written for the pooled (averaged) quantities. One cannot be sure what the effects of such a simplification(s) are in various coupled physical-biological models. Arguments can be made that such averaging may miss important effects (Frost, 1980), especially when different life stages react to the physical environment in different fashion--some swimming more vigorously than others, perhaps, or seeking different depths or light environments.

Both scaling and pooling are related to the basic question of how one measures components of a system; accordingly, the two might be related. Perhaps for certain ranges of some non-dimensional group (a group that incorporates both physical and biological quantities) all age classes can be pooled, or all species of, say, phytoplankton can be pooled. Similarly, more formal investigations into these questions may tell us whether we can average over certain space and time scales.

2. Predictability in a "chaotic" environment.

The consequences of coupling biological processes to a physical environment that has variability over a very broad range of space and time scales could be profound. There may be fundamental limits to predictability of biologically interesting quantities in such a "chaotic" environment. What such limits are, if any, is an important question with substantial ramifications. It may not be possible to predict beyond a certain point in time what the effects of changing global environments are upon marine animals, because of the fundamental limits to predictability in the coupled physical-biological systems of the sea. It may be possible to predict some quantities (e.g., biomass), but not others (e.g., abundance and distribution of individual species). Platt et al. (1977) considered this question when discussing models of phytoplankton productivity; and it seems profitable to extend their work. Perhaps there may be some guidance from more recent mathematical studies in nonlinear dynamics. Though it is not known whether the ocean as solely a physical system is chaotic (in the strict mathematical sense), one of the characteristics of chaotic (as opposed to deterministic) systems is a broad spectral range. This contrasts to the narrow "line"-type spectra found in deterministic systems. See Andereck et al. (1986).

The proposed approaches to both simplification and predictability are solely theoretical topics. This does not rule out applications to specific marine systems or populations of organisms, of course. Researchers should be encouraged to explore such applications of the ideas they develop.

B. Prototype Investigations of Biological Processes in Idealized Flows.

Biota are not mere passive tracers in the flows that characterize the sea's motions. At each life stage, an organism (planktonic or otherwise) will have behavioral responses, and will interact with the physical environment as well as other organisms. These facts, of course, make the totality of the GLOBEC program extremely complicated (and extremely interesting). The effects of specific flow regimes might be investigated by considering the behavior of, and interaction between, organisms in simple models for these flows. A researcher might select one from a number of common flow patterns (i.e., homogeneous, three-dimensional turbulence; organized coherent structures, like Langrnuir circulations; fronts and convergences; eddying structures; upwelling circulations; plumes; mixed zones and/or wakes around islands, to name several). Then, mimicking this prototype with simple, yet satisfying, physical dynamics, ask two kinds of questions. First, how do these flow regimes affect the biological properties one associates with individuals, or the properties one associates with single populations? For example, one might study the effects of small-scale turbulence on feeding success (Rothschild and Osborn, 1988). Another important phenomenon--aggregation into schools or swarms (Okubo, 1986), including the effects of such processes on feeding or predator avoidance--would be a likely candidate for investigation. Still another area for study might be how do flow patterns at a variety of spatial scales affect the transport of the larval stages of benthic invertebrates (Jackson and Strathmann, 1981; Possingham and Roughgarden, 1990). How is the success of settlement of these larvae on the shore affected? How important is this "settlement success" relative to competitive interactions on the shore between sessile adult organisms? Second, how do these flow regimes specifically affect populations that are coupled into communities? How, for example, are competitive interactions altered (Roughgarden, 1978)? How are trophic relations modified? Perhaps the effects on size class models (or size spectra models, a la Denman et al., 1989) can be approached in investigations such as these.

It is well to note four aspects of such prototype studies at this early "proposal" stage. First, there is the well-developed field of mathematical ecology that has been little utilized in oceanographic (and only slightly more in fisheries) investigations (see Roughgarden et al. [1989] for a modern perspective). Some insights from this previous work may be useful. Second, though it may be possible to mimic a few simple flow patterns analytically, numerical simulations of the dynamics (e.g., turbulence) will certainly be very useful in these types of investigations. We should encourage investigators to consider how their "simple" models might be generalized in future studies to more complex settings that would demand numerical simulation (or, perhaps, substantially greater computer resources). Third, many of the formulations for the behavior of, and interaction between, biota are only approximate, even within quite wide confidence limits. We should encourage researchers to consider carefully what such limits mean for the predictions they calculate--a "sensitivity analysis" for their efforts. Finally, these prototype studies are closely linked to the conceptual studies of simplification and predictability discussed above. The results of dimensional analyses of coupled physical-biological systems will surely form the bases for at least some of these prototype studies.

C. Site-Specific Models.

We propose a two-step process to attack the question of how the modifications we anticipate from a changing global climate will make themselves felt on **specific** animal populations at **specific** sites in the sea.

1. Now. The coastal ocean and the open sea.

The only realistic way to attack the problem of how to predict effects in the future is to understand the present. Accordingly, we focus on a specific problem at a specific site to see how well we can "put it all together". As an example, let us imagine compiling our "best" assessment of the biology of the individual life stages of a given species of, say, a copepod. Let us further construct the "best" model of the transport phenomena (advective plus mixing) at a site of limited extent, perhaps a coastal site. Then, given the observed physical forcing(s) plus the observed level(s) of predators upon the copepod stages (and prey items in the copepod diet) can we make a prediction about the concentration and distribution of the copepod population as the individuals progress through their life history? Recent work of this kind in the South Atlantic Bight (Hofmann, 1988) suggests that, so long as the time horizon is not too long, we may be closer to this specific goal than ever before.

Such attempts must be generalized to other environments, longer time horizons, and a variety of populations--benthic invertebrates, widely differing groups of holoplankton, and various fish and shellfish species. We target two "sites" initially: the upper ocean, anywhere on the globe, because it is so important biologically; and coastal sites, especially addressing questions that turn on cross-shelf transport. The coastal cross-shelf transport focus is important because transport across the continental shelf may be so crucially important to a wide variety of marine animals, especially benthic invertebrates (Roughgarden et al., 1989b), and larval fish and eggs (Checkley et al., 1988).

Three aspects of such models are immediately apparent. First, these studies will be dominated by numerical attempts, because only such efforts are likely to incorporate sufficient detail to be useful at specific sites. We should begin to think about ways to interact rapidly and efficiency with models that may have many tens of thousands of lines of code and are run at remote sites. We must insist that timely and constructive protocols allow us to interact quickly in a "predictor/corrector" mode. We anticipate taking advantage of the advances occurring in modeling of the upper ocean (e.g., the Price-Weller-Pinkel model [Price et al., 1986]) and modeling of coastal circulation (see particularly, E. Hofmann's coupled models in the South Atlantic Bight, referenced above). These efforts give us the confidence to continue the attempt to predict. Second, the incorporation of data into models is a critical topic that needs to be addressed early by any modeling attempt. The effort must be a cooperative one between empiricists (a measurement team) and modelers. This effort might assess the usefulness of the formal techniques of data assimilation (see Haidvogel and Robinson [1989], an entire journal issue devoted to this issue for oceanic modeling). These newer approaches have not been applied in biological models, whether coupled to the physical environment or not. Third, ensure that the "fit" between theory and measurement is good. For example, the output from present acoustic sensors is often a size-frequency spectrum. Will this quantity be easily extracted from multi-level, age-structured models? Is this the quantity we desire, and why? Similar remarks apply to the "fit" with remote sensed data, like ocean color, that appears to have great biological utility. Preparation for the use of time series data, perhaps from moored instruments, in more sophisticated ways than have previously been common in biological studies, should have a high priority for both empiricists and modelers.

2. Future predictions.

We have already alluded to one straightforward way in which the model studies we propose can be used to pursue the effects of global change. That is, drive the models with differing external forcing. For example, where a freshwater source of buoyancy is an important input, ask what circulation and transport patterns, as well as derived distributions of biota would result from the hypothesized shifts in rainfall or ice melt. Comparisons with the results of "present condition" models could be readily pursued. These results would be "short time scale" in the sense that the numerical simulations would be run only so long as the analyst believed that the flow patterns did not deviate substantially from observations--several weeks to a month, perhaps.

There may be ways to mimic climatologists' use of atmospheric GCMs (general circulation models) in the coastal ocean for "long time scale" assessments; that is, run the models for very long times until they reach "equilibrium", and then compare various equilibria (Mitchell, 1989). Such calculations have been performed for the ocean general circulation, but "the jury is still out" on how much confidence one should have in the results. Generalization of the same techniques to the coastal ocean is purely speculative at this time.

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